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Grazing promotes forb diversity across multiple communities in a California grassland

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Grazing promotes forb diversity across multiple communities in a California grassland

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Abstract

1. Forb species play a critical role in maintaining diversity and resilience in grasslands. Recent research has raised concerns that forb seed banks are declining in some areas, threatening this resilience under continued climate change. Cattle grazing has been shown to promote forb emergence in annual dominated grassland systems, yet forb responses to grazing remain highly variable and context dependent.
2. We assessed the effects of a conservation grazing program on forb abundance and diversity in an inner coastal California grassland, using paired grazed and ungrazed monitoring transects maintained for seven years across four distinct grassland communities. The grassland communities were categorized based on dominant species present, and included Harding grass, medusahead, mixed annual grassland, and native grassland. Across these grassland communities, we investigated the extent to which grazing influenced species richness, cover, diversity, evenness and community composition, focusing our analyses on all plant species, and specific groups of species: all forbs, native forbs, non-native forbs, and legumes (Fabaceae family). Grazing significantly increased forb richness and cover across the four grassland communities. Forb cover nearly doubled under grazing, while graminoid cover remained unchanged. Richness and cover of native forbs, non-native forbs, and legumes all significantly increased under grazing. Evenness decreased with grazing, indicating that grazed transects tended to have a few dominant species and many rare species. While the

responses of these groups of species were consistent across the four community types, there was no consistent shift in which species responded to grazing across communities.

3. Within each plot, we assessed how grazing influenced spatial variability, by comparing vegetation data across 10 quadrats along a transect. Grazing led to more consistent forb distribution across quadrats, reducing the spatial variability of forb cover within plots.
4. *Synthesis and applications:* This study demonstrates that a conservation grazing program can consistently promote forb richness and diversity across multiple grassland communities in an inner coastal California grassland. The specific forb species that responded to grazing were different in each community, but overall, the enhancement of forb diversity—including native forbs and legumes—increases the potential for replenishing diverse forb seed banks, leading to greater grassland resilience.

Introduction

There is growing attention to the critical role that forb species play in maintaining biodiversity and resilience in California's Mediterranean grasslands (Hayes and Holl 2003, LaForgia et al. 2018, Davy and Rinella 2019). Among the most biodiverse ecosystems in the state, California grasslands support approximately 90% of the state's rare and endangered plant and animal species and provide essential ecosystem services, including pollinator habitat, carbon storage, and livestock forage (Skinner and Pavlik 1994, Chaplin-Kramer et al. 2011, Huntsinger and Bartolome 2014, Dass et al. 2018). Forbs are key contributors to this diversity, with forb species richness four times greater than grass species richness (Sims and Risser 2000).

The arrival of Spanish colonizers and livestock in the 1700s (Heady 1988, Wagner 1989) initiated a transition in California grasslands to systems dominated by Mediterranean annual grasses. In the centuries that followed, native flora declined while invasive grasses spread, with additional changes driven by cropland conversion, overgrazing, and more recently, nitrogen deposition (D'Antonio et al. 2002; Seabloom et al. 2003). The transition to annual grass-dominated systems introduced greater vulnerability to disturbances that decrease grass seed production or increase grass seed mortality, as California annual grasses exhibit limited seed carryover between years (Heady 1958, Bartolome 1979). Many forb species, however, can persist in the seed bank for extended periods (Robertson and Hickman 2012) and opportunistically germinate when disturbances like grazing or fire create open gaps in the vegetation (Levine and Rees 2004, Kapás et al. 2020). Historically, the composition of forbs and grasses in California grasslands were likely shaped by periodic disturbances from native

ungulates (Hamilton 1997) and Indigenous burning (M. K. Anderson 2018), contributing to a pattern of episodic forb emergence and ongoing seed bank renewal (Saatkamp et al. 2014).

Grasslands with higher forb density in the seed bank have been shown to maintain plant cover during drought (Hallett et al. 2017) and following wildfire (Eviner and Cadenasso, in prep), as forbs compensate for the decrease in grass cover. However, recent research has raised concerns that forb seed banks are declining in some areas due to prolonged drought, nitrogen deposition and thatch accumulation from suppression of disturbance regimes (Harrison et al. 2015, Mariotte et al. 2017, Harrison et al. 2018, Eskelinen et al. 2021, Lesage et al. 2022). Such declines may threaten the resilience of grassland ecosystems under continued climate change (Harrison et al. 2015, Lesage et al. 2022). While overgrazing can degrade grasslands globally and in California (Fleischner 1994, Bestelmeyer et al. 2011), the suppression of disturbance regimes, such as fire and grazing, can also reduce diversity and inhibit forb emergence (D'Antonio et al. 2002, Weiss and Jeltsch 2015, Hernández et al. 2021). In disturbance-adapted ecosystems such as California grasslands, grazing with low to moderate stocking rates can promote forb cover and diversity (Safford and Harrison 2001, Stahlheber and D'Antonio 2013, Kapás et al. 2020). Increasingly, conservation grazing, a strategy that uses carefully targeted site-specific grazing regimes to benefit grassland ecology and conservation goals (Evans et al. 2023), has been employed to suppress non-native annual grasses and encourage native grass and forb establishment (D'Antonio et al. 2002, Coleman and Levine 2007, Davy and Rinella 2019, Molinari and D'Antonio 2020).

The response of forb abundance and diversity to grazing has been the focus of numerous studies in California grasslands, yet results remain highly variable and context-

dependent (Harrison et al. 2003, Stahlheber and D'Antonio 2013). Many studies report increases in forb cover and diversity under grazing (Rosiere 1987, Safford and Harrison 2001, Kimball and Schiffman 2003, Skaer et al. 2013), but responses often vary depending on forb groups, including species origin (native vs. non-native) (Harrison et al. 2003, Hayes and Holl 2003, Beck et al. 2015, Hernández et al. 2021) and the presence of leguminous species (Lavorel et al. 1999, Bartolome et al. 2007). Explanations for these differing responses are often attributed to variations in underlying ecological conditions such as soil type, climate, and disturbance history (Harrison et al. 2003, Stahlheber and D'Antonio 2013, Hallett et al. 2017). Although some studies have sought to identify consistent patterns in forb responses to grazing across landscapes (Hayes and Holl 2003, Skaer et al. 2013), few have examined these responses within inner coastal California grasslands spanning multiple grassland communities (but see Harrison et al. 2003).

Additionally, grazing can influence the spatial distribution of forbs within a grassland community in contrasting ways. Grazing may lead to greater similarity among patches by decreasing species preferred by grazers (Olff et al. 1999). Alternatively, under light grazing, increased patchiness in areas that are or are not grazed can result in increased spatial heterogeneity of species composition (Adler et al. 2001).

Given the variability in forb response to grazing, their documented declines in seed bank studies, and the important role forbs play in promoting resilience to environmental stressors such as drought and wildfire, further research is needed to evaluate how forbs respond to grazing in California's inner coastal grasslands. Here, we investigate whether consistent patterns

of forb response to grazing can be detected across four distinct grassland communities – those dominated by Harding grass, medusahead, mixed annual grasses, and native grasses.

In this study, we used seven plots with paired grazed and ungrazed monitoring transects established across four grassland communities throughout a 3,117 acre preserve in Sonoma County that employs a conservation grazing program. Specifically, we asked: (1) How does grazing alter overall vegetation and forb-specific richness, cover, diversity and species composition? (2) How does grazing affect spatial variability of forb cover within a plot? Does it enhance forb cover across patches, or lead to small-scale variability in vegetation? and (3) Among forbs, do responses vary based on species origin (native vs. non-native) or functional group (legume vs. non-legume)?

Methods

Study Location

This study was conducted at Pepperwood Preserve, which is located in the Southern Mayacamas Mountains in the Northern Coast Range near Santa Rosa, California (38.57°N, −122.68°W). The preserve encompasses 3,117 acres, about 30% of which are grasslands. Elevation ranges from 186 to 1,560 feet, with a Mediterranean climate, characterized by warm dry summers (mean high temperature of 22.2^{o}C) and mild wet winters (mean low temperature of 7.2^{o}C) (Western Regional Climate Center, 2025). The average annual precipitation is 815 mm per water year (1 October–30 September, CIMIS Weather Station, 34-yr average 1990–2025, Santa Rosa, California), and the precipitation during our study year was 732 mm for the water

year (1 October 2023–30 September 2024, CIMIS Weather Station, Santa Rosa, California). Grasslands within the preserve are primarily dominated by non-native annual grasses, but are interspersed with dense patches of the invasive perennial *Phalaris aquatica* (Harding grass), native perennial bunchgrasses such as purple needlegrass (*Stipa pulchra*) and California oatgrass (*Danthonia californica*), serpentine grasslands, and wet meadows (Gillogly et al. 2017).

Pepperwood Preserve has a documented history of cattle grazing since the mid 1800s. In 2013, the preserve implemented a conservation grazing program. Using an adaptive management strategy, rangeland managers adjust livestock density and grazing duration based on daily observations of soil disturbance, forage height, and animal condition, aided by electric fencing and portable water systems (Gillogly et al. 2014). Under this program, grazing timing and intensity vary across pastures each year, with stocking rates varying from 0-2.41 animal unit equivalent months, per acre (average of 0.69 AUM/acre from 2017 through 2024). The average AUM/acre in the season preceding data collection for this study was 0.34 AUM/acre. The preserve has experimented with year-round grazing in the past, however in 2024, the year of data collection for this study, cattle grazed the preserve from March through August, in 10–20 acre paddocks.

Study Design

In June 2017, seven permanent plots were established to determine the effects of grazing throughout the grasslands in the preserve. Within each of the seven plots are two parallel 55 meter transects, one of which is grazed, the second of which is ungrazed, within a

permanent exclosure that is approximately 26 x 60 meters. This experimental design allows us to identify trends that persist across local grassland communities and varying environmental conditions.

Plot locations were selected to capture the range of grassland plant communities and abiotic conditions, including elevation, slope, aspect, and soil types that are present within the preserve (Table 1). The preserve identified the most common grassland communities in which to distribute the array of plots. These include: two Harding grass plots dominated by *Phalaris aquatica* and a mix of non-native annual grasses and forbs; one medusahead plot dominated by *Elymus caput-medusae*, a mix of non-native annual grasses, and the native grass *Stipa pulchra*; two mixed annual grassland plots dominated by *Avena barbata* and a mix of other non-native annual grasses and forbs; and two native grassland plots dominated by *Danthonia californica*, non-native annual grasses, and forbs (Fig. 1). Grassland community compositional differences were tested using Bray-Curtis distances and two-way permutational multivariate analysis and were shown to differ significantly (PERMANOVA, $F_{3,10} = 1.83$, $p = 0.019$, Fig. 1).

Data Collection

We assessed vegetation composition along each transect within a plot by sampling ten 1 m^2 quadrats placed at five-meter intervals, alternating sides of the transect tape. Within each quadrat, species were identified, and percent cover was estimated for each species using Daubenmire bins (Daubenmire 1959). Vegetation covers often totaled above 100%. Because

California grassland species can vary greatly in their flowering phenology, vegetation composition was assessed at four different time points, to capture the full suite of species emerging over the course of the growing season.

The first monitoring event took place in early April 2024, targeting early-season forbs and forb cover prior to grass cover obscuring the forb understory. To facilitate species identification, electric fences were established around grazed transects to exclude cattle on April 1st. While early season sampling may have missed species that had not yet recovered from grazing, by the mid and late season surveys the vegetation had largely recovered. A second round of monitoring was conducted in early May 2024, to capture peak flowering of most forb and grass species. Monitoring was repeated in early June 2024, to document later-season grasses and peak grass cover, and a final round of monitoring was conducted in early August 2024, to record any late-summer flowering forbs. Data across time points was compiled by recording the highest percent cover observed for each species across any of the four monitoring events.

Data Analysis

All analyses were performed in statistical software R version 4.4.1 (R Core Team 2024). Normality was assessed using Shapiro–Wilk tests and visual inspection of Q–Q plots. When data did not meet normality assumptions, nonparametric tests were used. Most analyses in this study were conducted using nonparametric statistical tests due to high variability in species composition and cover across the different grassland communities sampled.

Richness and Cover

To evaluate the effects of grazing on species richness and percent cover, we used generalized linear mixed models (GLMMs) to account for the hierarchical structure of the data and non-normal distribution of percent cover values. Treatment (grazed or ungrazed) was established as the fixed effect with 'ungrazed' as the reference level. Richness and percent cover were calculated at the quadrat level, and plot was included as a random effect to account for variability among the different grassland communities sampled. The sum of unique species across all ten quadrats per transect was also calculated, and showed similar trends to quadrat-level richness, so is not presented here.

We fitted models to distribution families based on the distribution of the data, comparison of model fit using Akaike's Information Criterion (AIC), and assessment of model residuals in the "*glmmTMB"* package (Brooks et al. 2017). Specifically, we used a negative binomial distribution for forb, non-native forb and legume richness, a poisson distribution for graminoid and total species richness, and a zero-inflated poisson distribution for native forb richness. For percent cover comparisons, we used a Tweedie distribution for forb cover, non-native forb cover, and legume cover, a Gaussian distribution for graminoid cover, and a zero-inflated beta distribution for native forb cover. Graminoids were largely composed of grass species, with two species in the Cyperaceae family and four species in the Juncaceae family. In addition to the GLMMs, we used Wilcoxon signed rank paired tests to compare mean richness and mean percent cover between grazed and ungrazed paired transects within each plot.

Diversity, Evenness & Variability

We also evaluated Simpson's diversity and evenness indices, which incorporate both species richness and the proportional abundance of each species, giving greater weight to common species and less to rare ones. We then compared Simpson's diversity and evenness between the grazed and ungrazed transects, using GLMMs with the same model structure as above, and a Beta distribution in the "*glmmTMB"* package (Brooks et al. 2017).

We also evaluated how grazing affects spatial variability of forbs across quadrats within each transect. To do this, we calculated the coefficient of variation (CV) of percent forb cover for each transect by dividing the standard deviation of forb cover values across the ten quadrats by their mean. This yielded one CV value for each grazed and ungrazed transect. We then used a Wilcoxon signed rank test to compare CVs of the grazed and ungrazed transects.

Species Composition

To evaluate patterns in plant community composition, we conducted a non-metric multidimensional scaling (NMDS) ordination with a Bray–Curtis dissimilarity matrix using the "*metaMDS"* function in the "*vegan"* package (Oksanen et al. 2025). To test for differences in species composition, we ran two separate permutational multivariate analyses of variance (PERMANOVAs; Anderson 2001). The first PERMANOVA tested for differences in community composition among the four grassland communities sampled in this study. The second

PERMANOVA tested for differences in species composition between grazed and ungrazed transects across all grassland communities. Species occurring in fewer than 10% of quadrats were excluded from the analysis to reduce the influence of rare species. Both tests were conducted using Bray–Curtis dissimilarities with 999 permutations with the "*adonis2"* function of the "*vegan"* package (Oksanen et al. 2025).

To assess differences in multivariate dispersion (beta diversity) across quadrats within grazed and ungrazed transects, we performed a permutational analysis of multivariate dispersions (PERMDISP; Anderson 2006). This analysis was based on Bray–Curtis dissimilarities, using the "*betadisper"* function in "*vegan"*, with significance assessed by 999 permutation tests.

To identify species that were significantly associated with either grazed or ungrazed transects, we conducted an indicator species analysis using the "*multipatt"* function in the "*indicspecies"* package (De Cáceres and Legendre 2009). The analysis was based on species percent cover data and used the "*IndVal.g"* statistic to quantify the strength of association between each species and the grazed or ungrazed treatment groups. Statistical significance was assessed with 999 permutations.

Results

Even with significant differences in community composition among grassland types (PERMANOVA, $F_{3,10} = 1.83$, $p = 0.019$, Fig. 1), grazing significantly increased the means of total species richness (GLMM, $z = -3.17$, $p = 0.002$, Fig. 2a) and forb richness (GLMM, $z = -5.80$, $p = 0.003$, Fig. 2a). This response was also evident when directly comparing each paired grazed and ungrazed transect, although the magnitude of responses varied across plots (Figs. 2b, 2c). The

increase in total species richness was primarily driven by forbs. While graminoids dominated in cover (Fig. 3a), they comprised only 28% of total species richness, with no significant difference in graminoid species richness between treatments (GLMM, $z = -1.36$, $p = 0.175$, Fig. 2a).

There was also no significant difference in graminoid cover with grazing (GLMM, $z = -0.855$, $p = 0.393$, Fig. 3a). In contrast, forb cover nearly doubled under grazing, increasing on average by a factor of 1.96 (GLMM, $z = -3.97$, $p < 0.001$, Fig. 3a), which is also reflected in the paired transect means (Fig. 3b). As a result, the ratio of forbs to graminoids shifted substantially with grazing. Graminoid cover was on average 35% higher than forb cover in grazed transects, compared to 169% higher in the ungrazed transects (Fig. 3a).

In addition to increases in richness and cover, forbs were more evenly distributed across quadrats within grazed transects. This was indicated by a significantly lower coefficient of variation for forb percent cover in grazed transects (Wilcoxon rank sum, $p = 0.029$, Fig. 3c).

Higher species richness and forb cover in grazed transects were reflected in higher Simpson Diversity Index values for all species (GLMM, $z = -2.49$, $p = 0.013$, Fig. 4a), and forb species (GLMM, $z = -2.18$, $p = 0.029$, Fig. 4a). However, Simpson Evenness decreased in the grazed transects for all species (GLMM, $z = 2.05$, $p = 0.039$, Fig. 4b) and forb species (GLMM, $z = 2.61$, $p = 0.009$, Fig. 4b), indicating that the increases observed in forb richness were due to a higher number of low-abundance species.

In both grazed and ungrazed transects, non-native forbs had higher species richness (Fig. 5a) and cover (Fig. 6a) than native forbs. Grazing increased the richness of both native (Figs. 5a, 5b) and non-native (Figs. 5a, 5c) forbs to the same degree (GLMM, $z = -2.09$, $p = 0.037$ for native forbs; $z = -2.05$, $p = 0.040$ for non-native forbs). Grazing also increased the percent cover

of both native (Figs. 6a, 6b) and non-native (Figs. 6a, 6c) forbs. Native forb cover increased from 8.3% to 24.5% average cover (GLMM, $z = -2.54$, $p = 0.007$, Fig. 6a), while non-native forb cover increased from 49.2% to 82.7% average cover (GLMM, $z = -2.71$, $p = 0.011$, Fig. 6a). Similar patterns were evident when directly comparing cover of transect pairs, although the magnitude of responses varied (Figs. 6b, 6c). One of the mixed annual grassland plots (MIX1) and one of the Harding grass dominated plots (HAR2) decreased in native forb cover with grazing (Fig. 6b), and one of the native grassland plots (NAT3) decreased in non-native forb cover with grazing (Fig. 6c).

Legumes comprised 25% of the forb species recorded in the study. Similar to forbs overall, grazing significantly increased legume richness (GLMM, $z = -3.32$, $p = 0.001$, Fig. 5a) and percent cover (GLMM, $z = -3.59$, $p < 0.001$, Fig. 6a). This response was further supported by our findings from an Indicator Species Analysis. Out of the 133 species recorded, one native leguminous species, miniature lupine (*Lupinus bicolor*), was identified as a significant positive responder to grazing across grassland communities (Indicator Value = 0.87, $p = 0.025$).

While grazing increased forb diversity, decreased evenness, and led to more consistent forb cover within transects, it did not produce uniform shifts in species composition across grassland communities. Although broad plant groups showed clear responses to grazing, an NMDS ordination based on Bray-Curtis distances across all plots indicated no significant difference in overall species composition between grazed and ungrazed treatments (PERMANOVA, $F_{1,12} = 0.943$, $p = 0.507$). Similarly, grazing had no effect on beta diversity, or the variability of species composition across quadrats within a given plot (PERMDISP, $p = 0.702$).

When examining species composition within plots, there was an average of 58% similarity between paired grazed vs. ungrazed transects (Table 2), suggesting that there were moderate, localized differences in composition between treatments. To help further characterize species-specific responses to grazing, we compiled lists of species found exclusively in grazed transects (Table 3), exclusively in ungrazed transects (Table 4), and those with a change in absolute cover of greater than 10% between treatments (Table 5). Among species found exclusively in grazed or ungrazed transects, none occurred in more than three out of seven pairs, and the majority of species were restricted to a single plot (Tables 3, 4), underscoring the high compositional variability across plots. The species that showed the greatest change in percent cover with grazing (Table 5) were consistent with the broader plant group responses to grazing. Five native species (including three forbs) increased by greater than 10% with grazing, while three natives (including one forb) decreased by greater than 10% with grazing (Table 5). Native forbs also represented a large proportion of species unique to grazed transects, accounting for 85% of species only found in the grazed transects (Table 3), and 44% of species only found in the ungrazed transects (Table 4). Legumes made up 20% of species found exclusively in grazed transects (Tables 3).

Discussion

Identifying management strategies to protect and increase robust forb communities is paramount to ensuring the long term resilience of California grassland systems, especially under intensifying environmental stressors due to climate change (Hallett et al. 2017, LaForgia et al. 2018, Eviner and Cadenasso in prep). Moderate livestock grazing is one potential tool to support

forb abundance and diversity (Hayes and Holl 2003, Díaz et al. 2007, Stahlheber and D'Antonio 2013, Bartolome et al. 2014), but previous research shows forb responses to grazing are highly variable (D'Antonio et al. 2002, Harrison et al. 2003, Stahlheber and D'Antonio 2013). Here, we show that a conservation grazing regime in an inner coastal grassland led to consistent increases in forb richness, cover and diversity across multiple grassland communities, offering a scalable intervention to conserve and restore California grasslands.

Our findings align with previous studies demonstrating that moderate grazing can promote increased forb diversity and cover (Hayes and Holl 2003, Stahlheber and D'Antonio 2013, Skaer et al. 2013). Several mechanisms may explain this response. Even when forb seeds are present in the seed bank, successful establishment is hindered by thatch build up and competition from annual grasses (Brandt and Seabloom 2012). Grazing reduces live biomass, altering competitive interactions among plant species, and decreases litter and thatch accumulation, increasing light availability at the soil surface and facilitating forb germination (D'Antonio et al. 2002, Coleman and Levine 2007, Molinari and D'Antonio 2020).

Beyond impacting forb establishment, grazing shapes how forbs are distributed across space. These effects vary depending on the grazing regime, existing vegetation, topography, and the scale of observation. Patchy grazing in uniform vegetation tends to increase heterogeneity, whereas uniform grazing in naturally patchy vegetation can lead to homogenization (Adler et al. 2001). At our study site, grazing led to more consistent distribution of forbs across grazed patches within plots, reflected by lower coefficients of variation in forb cover. Greater consistency in forb cover could lead to a more evenly distributed seed bank, enhancing the system's resilience, particularly in response to patchy disturbances.

When we examined forb group responses, clear patterns also emerged. Across grassland communities, legumes, native forbs, and non-native forbs all showed consistent increases in richness and cover under grazing. In our study, legumes accounted for 25% of forb species, and their increase in richness and cover with grazing is consistent with patterns reported elsewhere (Noy-Meir and Kaplan 2002). While some studies report declines in native species under light to moderate spring grazing (Gornish and Ambrozio dos Santos 2016), our findings align with research reporting positive effects of grazing on both native and non-native forbs (Hayes and Holl 2003, Davy and Rinella 2019). These contrasting outcomes underscore the importance of background abiotic conditions, land-use history, and grazing regimes in shaping forb responses (Harrison et al. 2003, Stahlheber and D'Antonio 2013). Several studies have found greater increases in native forb richness with grazing on resource-limited serpentine soils compared to non-serpentine (Harrison et al. 2003, Beck et al. 2015, Hernández et al. 2021), and more positive native forb responses in interior than coastal grasslands (Stahlheber and D'Antonio 2013).

While our study showed consistent grazing effects on forbs as a whole and specific forb groups, we found no uniform shift in which species responded to grazing across communities. *Lupinus bicolor* was the only species to consistently increase in response to grazing across grassland communities, a finding also reported in other studies (Thomsen et al. 1993). While legumes generally improve forage quality, *L. bicolor* is toxic to livestock (Forero et al. 2011), and toxic plant species can increase under grazing due to herbivore avoidance (Briske 1996, Milchunas and Noy-Meir 2002). With this exception, the species that responded to grazing varied among grassland communities. This is highlighted by our observation that among the

species that exclusively appeared in grazed (Table 3) or ungrazed (Table 4) transects, the majority appeared in only one of the seven plots.

Although each community type had specific species that responded to grazing, there were changes in species evenness patterns detected across communities. Evenness decreased with grazing, suggesting that increases in diversity were largely driven by increases in low-abundance species, as highlighted by the one-time occurrence of many species unique to the grazed transects. The response of evenness to grazing can vary. Grazing can increase richness and evenness through reducing more dominant plants, creating opportunities for less common species to establish. Furthermore, selective consumption by grazers can favor species that grazers avoid, increasing their dominance (Olff and Ritchie 1998). The evenness patterns we observed, combined with increaeses in richness and diversity, suggest that light to moderate grazing regimes did not not substantially reduce the dominance of common species, but instead created space for rarer species to establish.

Increasing the presence of rarer species can provide several important benefits. Even low-abundance forbs can produce substantial amounts of seed, replenishing the seed bank and supporting future establishment of rare species (Brandt and Seabloom 2012). Moreover, modest increases in richness of low-abundance forb species can enhance ecosystem functions, such as pollination services (Orford et al. 2016). The high species richness and consistent forb cover we observed across grazed transects suggest potential for diverse forb recruitment and seed bank renewal of rarer species. These contributions are especially valuable in California grasslands, which are among the most heavily invaded ecosystems in the world (Seabloom et al. 2003). Increasing diversity, particularly among native species, remains a significant ecological

challenge (D'Antonio et al. 2002, Harrison et al. 2003, Coleman and Levine 2007, Hernández et al. 2021).

From a management perspective, grazing may still be beneficial even when it increases the proportion of non-native forbs, because it can still suppress highly invasive grasses while enhancing overall forb richness and diversity. For example, Stein et al. (2014) found that when the invasive grass medusahead was replaced by non-native forbs, ecosystem services such as forage quality improved. Reducing invasive annual grasses can also lower wildfire risk, as their fine, continuous fuels can increase fire frequency (D'Antonio and Vitousek 1992). Future research that evaluates the ecological roles of non-native forbs and develops strategies to balance their functional benefits with invasive species control will be key for maximizing the conservation potential of grazing in California grasslands.

Our findings showed that within a single preserve spanning several grassland communities, a conservation grazing regime consistently led to increased forb diversity, with species composition reflecting the distinct species pools of each grassland community. The overall increase in forb diversity expands the potential for replenishing a diverse and resilient seed bank – a critical foundation for maintaining grassland health amid ongoing environmental change.

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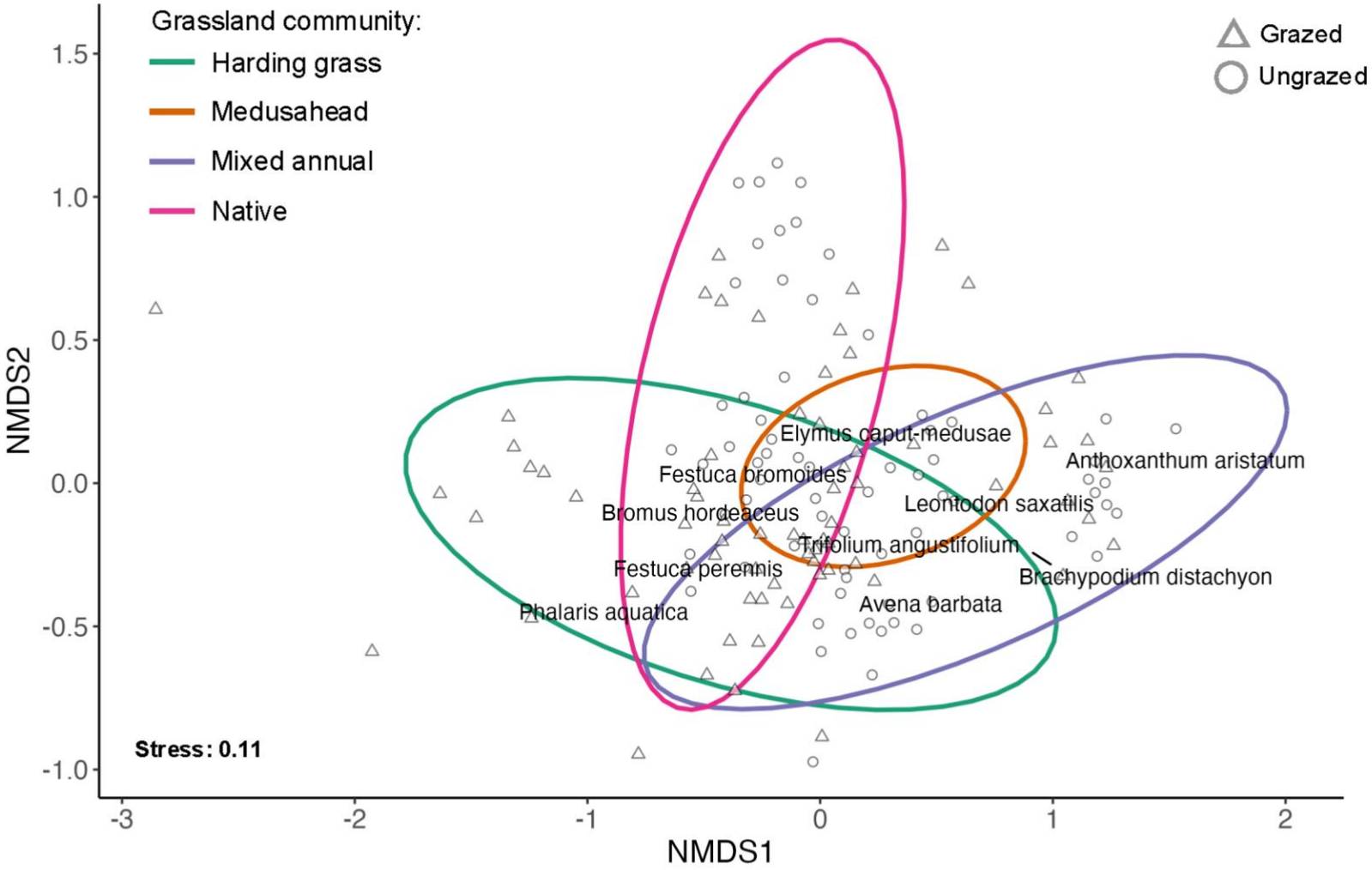

Fig. 1 Nonmetric multidimensional scaling (NMDS) plots for differences in species composition between grassland communities at Pepperwood Preserve with 95% confidence ellipses displayed, colored by grassland community. The points represent quadrats, with shapes indicating grazed or ungrazed. The distance between any two points represents the difference in community composition (Bray–Curtis dissimilarity index). The ten species with the highest average abundance across all plots in the study are projected. PERMANOVA results suggest that species composition did vary significantly by grassland community ($F_{3,10}$ =1.83, p = 0.019).

Table 1. Seven paired grazed and ungrazed plots at Pepperwood Preserve were evaluated in this study. Plots were established across grassland communities and a range of abiotic conditions with varying aspect, elevation, slope and soil type.

Grassland	*Plot*	*Aspect*	*Average Elevation (ft)*	*Avg Slope %*	*Soil Type*
Harding grass	HAR01	S	1166.8	19.9%	Yorkville Clay Loam
Harding grass	HAR02	E	1411.1	22.5%	Yorkville Clay Loam
Medusahead	MED03	W	1233.9	19.3%	Yorkville Clay Loam
Mixed annual grassland	MIX01	E	1371.1	19.9%	Yorkville Clay Loam
Mixed annual grassland	MIX10	SW	414.0	15.8%	Spreckels Loam
Native grassland	NAT03	N	1395.8	24.0%	Yorkville Clay Loam
Native grassland	NAT04	W	1217.3	15.8%	Yorkville Clay Loam

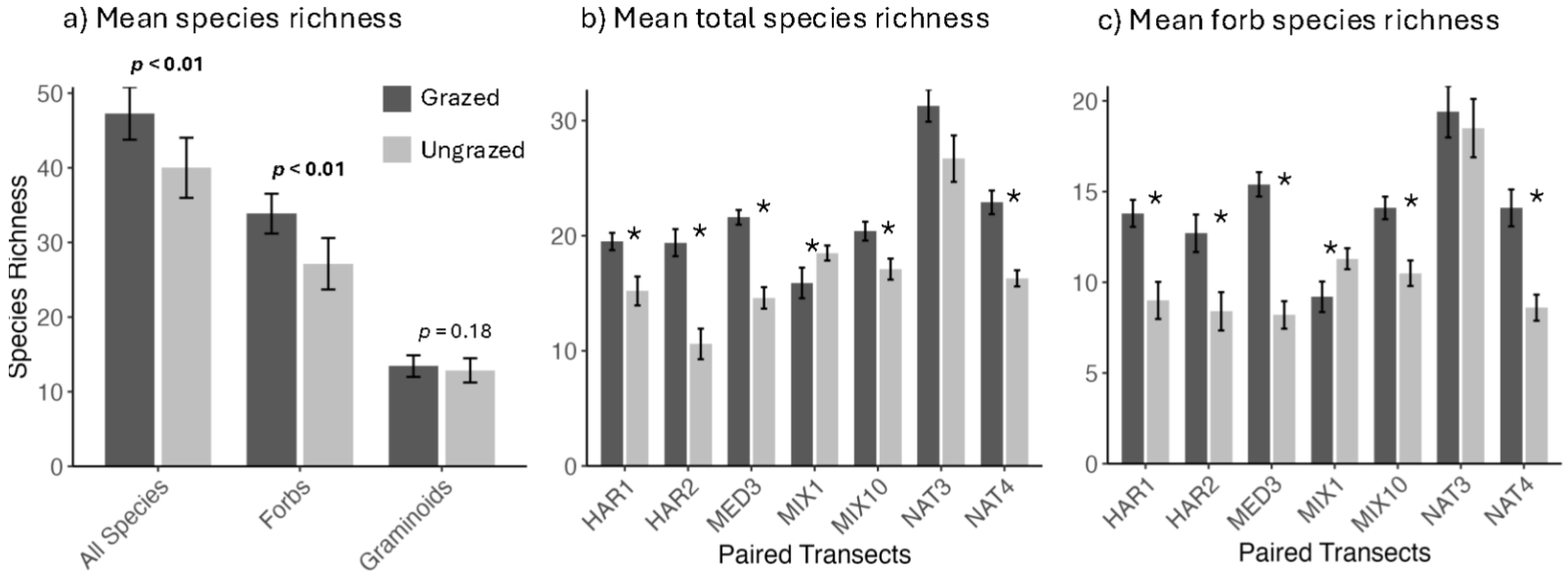

Fig. 2 Species richness was calculated by taking the means of the ten quadrats for each transect. (a) Mean species richness and standard error of grazed and ungrazed transects for all species, forbs, and graminoids. Bolded p values indicate significant differences for generalized linear mixed models with an alpha ≤ 0.05. (b) Mean total species richness and standard error by paired transects. (c) Mean forb species richness and standard error by paired transects. In b and c, * indicates significant differences in richness between paired grazed and ungrazed transects using Wilcoxon signed rank tests with an alpha ≤ 0.05. X-axis labels in b and c represent the names of plots with paired transects (HAR = Harding grass, MED = medusahead, MIX = mixed annual grassland, and NAT = native grassland).

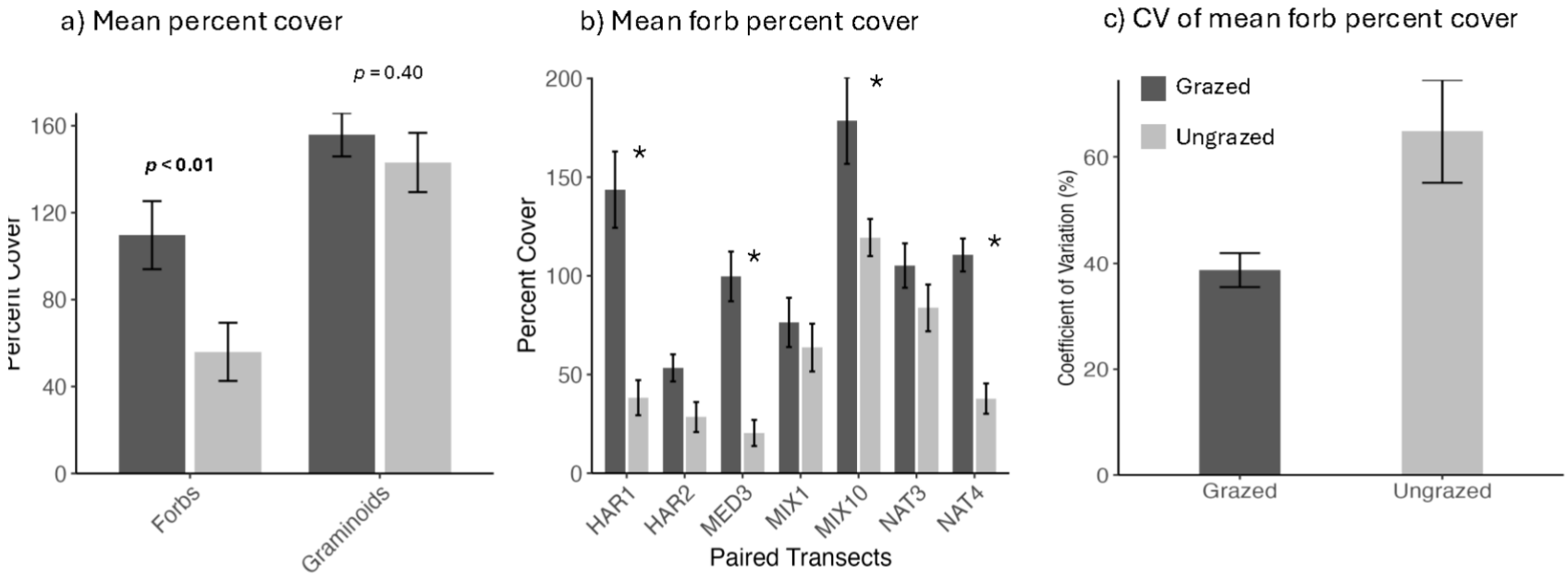

Fig. 3 Percent cover was calculated by taking the means of the ten quadrats for each transect. (a) Mean percent cover and standard error of grazed and ungrazed transects for forbs and graminoids. Bolded p values indicate significant differences for generalized linear mixed models with an alpha ≤ 0.05. (b) Mean percent cover and standard error of forb cover by paired transects. * indicates significant differences in cover between paired grazed and ungrazed transects using Wilcoxon signed rank tests with an alpha ≤ 0.05. X-axis labels represent the names of plots with paired transects (HAR = Harding grass, MED = medusahead, MIX = mixed annual grassland, and NAT = native grassland). (c) Coefficient of variation (CV) and standard error for the percent cover of forbs between grazed and ungrazed transects. CV was significantly lower in the grazed plots, indicating a more consistent distribution of forb cover with grazing (Wilcoxon rank sum, $p = 0.029$).

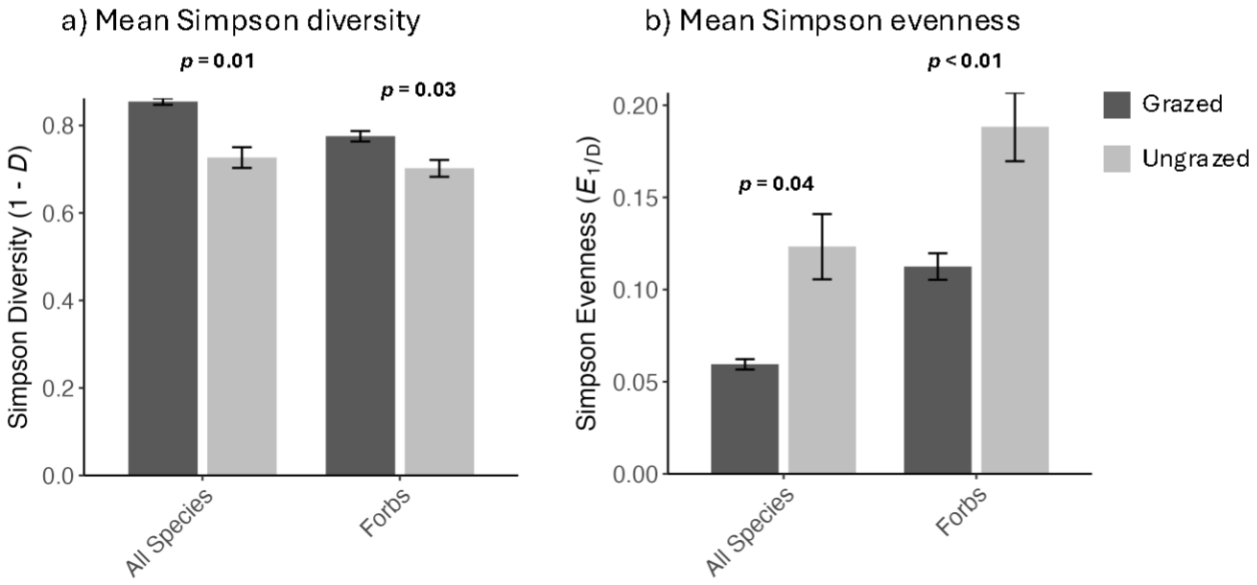

Fig 4. (a) Mean Simpson diversity and standard error between grazed and ungrazed transects for all species and forbs. (b) Mean Simpson evenness and standard error between grazed and ungrazed transects for all species and forbs. In a and b, bolded p values indicate significant differences for generalized linear mixed models with an alpha ≤ 0.05.

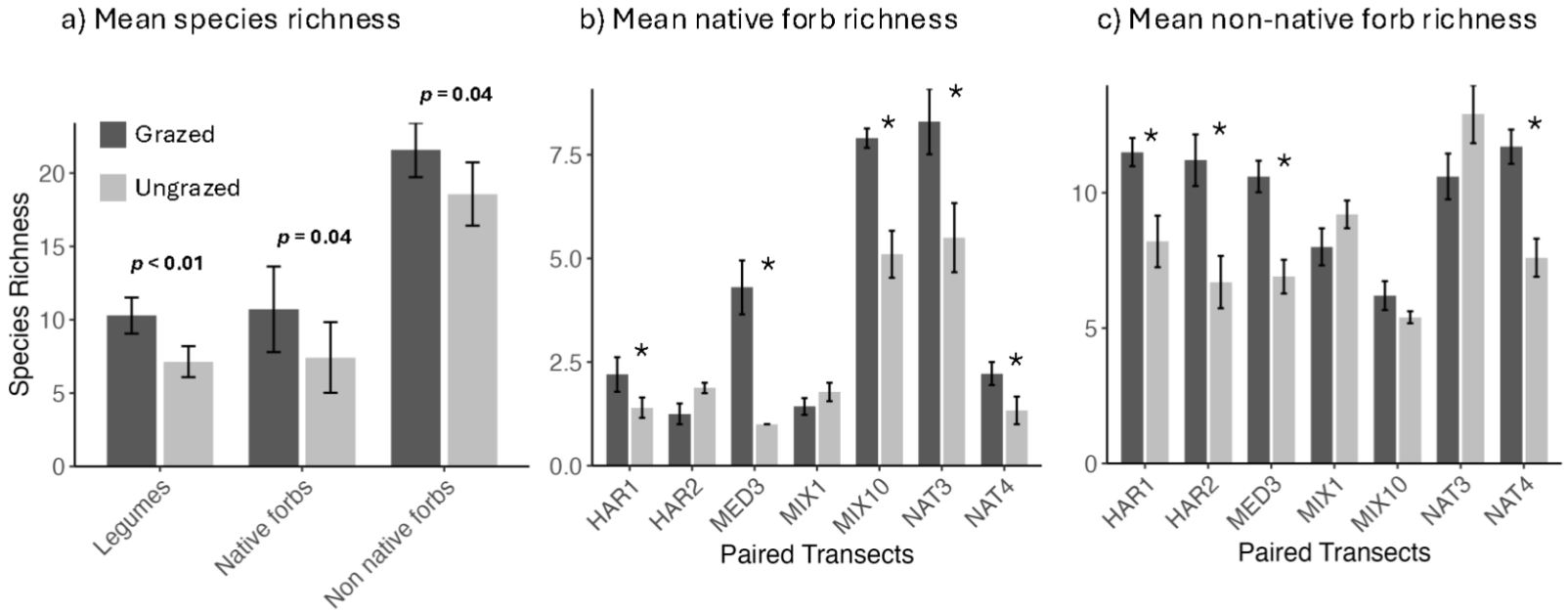

Fig. 5 Species richness was calculated by taking the means of the ten quadrats for each transect. (a) Mean species richness and standard error of grazed and ungrazed transects for legumes, native forbs and non-native forbs. Bolded p values indicate significant differences for generalized linear mixed models with an alpha ≤ 0.05. (b) All species richness and standard error by paired transects. (c) Forb species richness and standard error by paired transects. In b and c, * indicates significant differences in richness between paired grazed and ungrazed transects using Wilcoxon signed rank tests with an alpha ≤ 0.05. X-axis labels in b and c represent the names of plots with paired transects (HAR = Harding grass, MED = medusahead, MIX = mixed annual grassland, and NAT = native grassland).

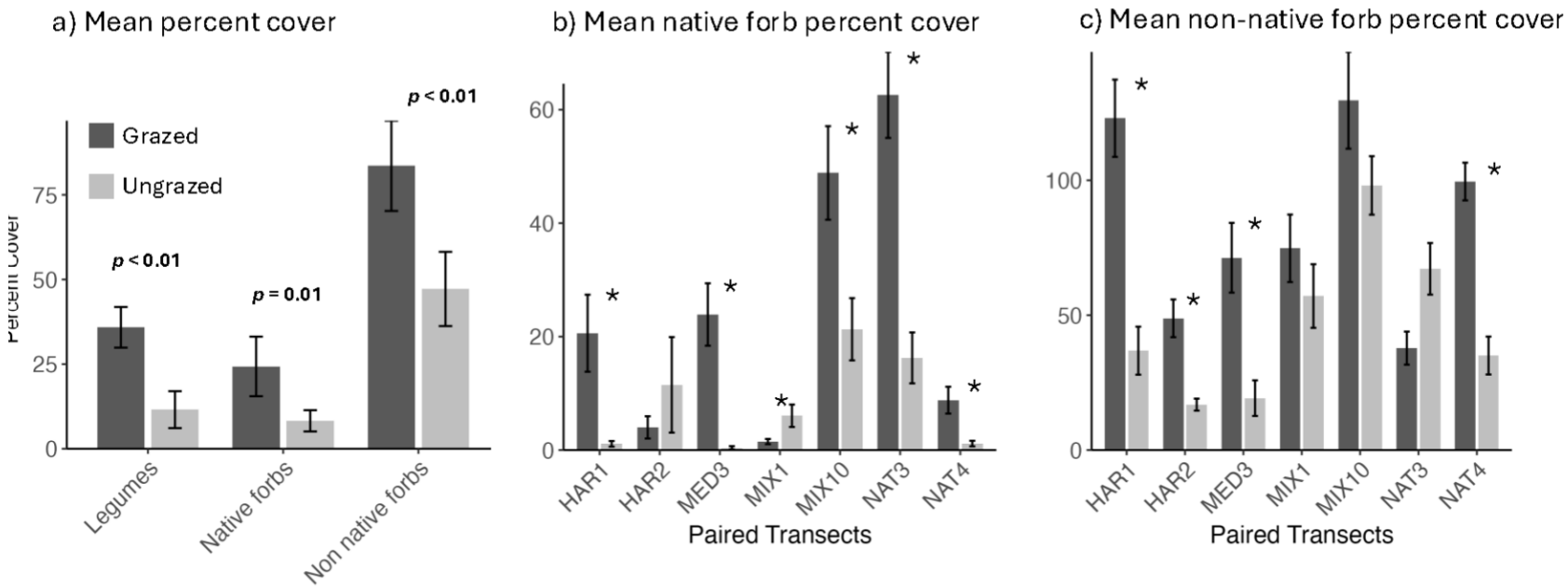

Fig. 6 Percent cover was calculated by taking the means of the ten quadrats for each transect. (a) Mean percent cover and standard error of grazed and ungrazed transects for legumes, native forbs, and non-native forbs. Bolded p values indicate significant differences for generalized linear mixed models with an alpha ≤ 0.05. (b) Mean percent cover and standard error of native forbs by paired transects. (c) Mean percent cover and standard error of non-native forbs by paired transects. In b and c, * indicates significant differences in richness between paired grazed and ungrazed transects using Wilcoxon signed rank tests with an alpha ≤ 0.05. X-axis labels in b and c represent the names of plots with paired transects (HAR = Harding grass, MED = medusahead, MIX = mixed annual grassland, and NAT = native grassland).

Table 2. Percent similarity of species richness between the grazed and ungrazed transects for each plot. Average percent similarity across all plots is 58%.

Paired Plots	*Shared Species*	*Total Species*	*Percent Similarity*
HAR01	26	43	60%
HAR02	26	58	45%
MED03	27	52	52%
MIX01	31	48	65%
MIX10	35	49	71%
NAT03	50	80	63%
NAT04	30	56	54%
Average % similarity			**58%**

Table 3. Species that exclusively appeared in the grazed transects. The majority consist of native forbs. Non forb species are bolded, * indicates leguminous species.

Species Name	*Origin*	*Frequency found in transects*	*Mean cover across transects*
*Acmispon wrangelianus**	Native	3/7	13.0%
*Acmispon americanus**	Native	3/7	3.4%
Grindelia hirsutula	Native	2/7	7.2%
Petrorhagia dubia	Non-native	2/7	0.5%
Juncus xiphioides	**Native**	**1/7**	**63.5%**
Achillea millefolium	Native	1/7	15.5%
*Trifolium fucatum**	Native	1/7	13.8%
Chlorogalum pomeridianum	Native	1/7	9.3%
Triphysaria pusilla	Native	1/7	9.3%
Calystegia collina	Native	1/7	8.4%
Centromadia fitchii	Native	1/7	4.0%
Micropus californicus	Native	1/7	3.0%
Ranunculus muricatus	Native	1/7	3.0%
Sidalcea diploscypha	Native	1/7	1.9%
Perideridia kelloggii	Native	1/7	1.9%
Primula hendersonii	Native	1/7	1.9%
Bromus carinatus	**Native**	**1/7**	**0.5%**
Daucus pusillus	Native	1/7	0.5%
Pseudognaphalium californicum	Native	1/7	0.5%
*Trifolium oliganthum**	Native	1/7	0.5%

Table 4. Species that exclusively appeared in the ungrazed transects. All are forbs. * indicates leguminous species.

Species Name	*Origin*	*Frequency found in transects*	*Mean cover across transects*
Aphanes occidentalis	Native	2/7	1.3%
Rumex acetosella	Non-native	1/7	38.0%
Centaurea solstitialis	Non-native	1/7	15.5%
Cardamine oligosperma	Native	1/7	0.9%
Anthriscus caucalis	Non-native	1/7	0.5%
Clarkia purpurea	Native	1/7	0.5%
Galium aparine	Native	1/7	0.5%
Stellaria media	Non-native	1/7	0.5%
*Trifolium campestre**	Non-native	1/7	0.5%

Table 5. Species that exhibited greater than 10% absolute change in cover due to grazing. Species are sorted by highest to lowest mean cover in the grazed transects. Non forb species are bolded, * indicates leguminous species.

Species Name	*Origin*	*Mean cover grazed*	*Mean cover ungrazed*	*Change in cover with grazing*	*Increase (↑) or decrease (↓) with grazing*
Leptosiphon jepsonii	Native	29.3%	3.0%	26.3%	↑
Phalaris aquatica	**Non-native**	**29.0%**	**63.9%**	**-34.9%**	↓
Plantago lanceolata	Non-native	27.5%	10.5%	17.0%	↑
Briza maxima	**Non-native**	**27.5%**	**1.1%**	**26.4%**	↑
Hedypnois rhagadioloides	Non-native	23.0%	0.5%	22.5%	↑
Ranunculus occidentalis	Native	19.8%	5.5%	14.3%	↑
Madia gracilis	Native	18.6%	4.0%	14.6%	↑
Juncus occidentalis	**Native**	**17.6%**	**6.6%**	**11.0%**	↑
Juncus bufonius	**Native**	**15.8%**	**3.0%**	**12.8%**	↑
Festuca bromoides	**Non-native**	**13.2%**	**23.4%**	**-10.2%**	↓
*Trifolium hirtum**	Non-native	5.0%	19.1%	-14.1%	↓
Holcus lanatus	**Non-native**	**3.0%**	**63.5%**	**-60.5%**	↓
Festuca idahoensis	**Native**	**1.8%**	**26.8%**	**-25.0%**	↓
Baccharis pilularis	**Native**	**0.5%**	**43.0%**	**-42.5%**	↓
Achyrachaena mollis	Native	0.5%	15.5%	-15.0%	↓